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## EXPERIMENTAL STUDIES ON THE DURATION OF LIFE

### I. INTRODUCTORY DISCUSSION OF THE DURATION OF LIFE IN *DROSOPHILA*<sup>1</sup>

RAYMOND PEARL AND SYLVIA LOUISE PARKER

SUCH quantitative knowledge as exists of fundamental principles in the general biology of the duration of life has, in the main, been derived from an examination by purely statistical methods of human mortality records. Of course a good deal of information about the biology of death and duration of life of a general and non-quantitative character has been gained from experimental work on lower organisms. This literature has recently been reviewed by one of us (Pearl (1) to (7) inclusive). But the outstanding fact is that most of the existing *quantitative* data about duration of life are purely statistical, and derived from man as material.

The statistical method of acquiring knowledge of natural phenomena has a number of distinct and important limitations (cf. Pearl (8)). It is the settled policy of this department to check every conclusion drawn from purely statistical methods by an independent experimental investigation of the same problems, wherever in the nature of the case this is possible. Most problems of human vital statistics can not, in the nature of the case, be investigated experimentally, in any direct way with man himself as material. Probably this is chiefly the reason why all of the immense mass of data collected, and work done upon vital statistics has contributed so little in the

<sup>1</sup> Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University, No. 45.

way of general principles to the science of biology. In outlining the plans of the department at the time of its inauguration provision was made, as a major element in the whole organization scheme, for experimental work on the duration of life, to parallel as closely as possible, in respect of its problems and foci of interest, the statistical work of the department. The present paper is the first of a series which will appear dealing with the experimental side of our work.

Originally it was planned to use mice as the material for experimentation on the duration of life, and a large and flourishing colony was bred up in accordance with the most critical genetic standards for experimental material. Just as the colony was ready to start definitive experimentation with, an accident completely destroyed it.

It was then decided, after advising with a number of persons, notably Professor T. H. Morgan and Dr. Jacques Loeb, to take up *Drosophila* as material for the extensive program of experimental work which we had planned. This organism has the great advantage over any other which could be used, that its genetic behavior and potentialities are more thoroughly understood than those of any other animal, thanks to the epoch-marking researches of Morgan (9) and his students. It has the further great advantage that under certain conditions, which we now rather clearly understand, its duration of life, both in respect of means and of the  $l_x$  or  $d_x$  distributions of a life table, is extraordinarily like that of man, with one day in the life of the fly corresponding roughly to one year in the life of man.

The first paper in the series aims to present, as a background of reference for further contributions, the following essential items:

1. A brief review of what has been noted by previous workers regarding duration of life in *Drosophila*, and other insects in so far as the observations are quantitative in character.

2. The details of our material and methods of exper-

imentation, which are critically standardized and have been used in the work which will be described in subsequent papers.

3. The general form and characteristics of the mortality curves of *Drosophila*, presenting mortality tables for certain strains.

4. The influence of certain phases of the experimental technique employed upon the results.

Specific problems regarding the duration of life will be presented and discussed in the subsequent papers in the series.

#### LITERATURE

The earliest mention we have found of observations on the duration of life of *Drosophila* is a casual reference in a paper by Moenkhaus (10) published in 1911 in which he makes the following statement in connection with egg counts: "We have kept females alive 153 days." There are no details of any kind, as to conditions or numbers involved.

The first paper to make more than casual reference to the duration of life of *Drosophila* is a paper published in 1913 by Hyde (11). In studying fertility and sterility in different strains of flies he found two strains which differed to a marked degree in respect of length of life, and made crosses to study the behavior of the shorter length of life of the mutant "truncate" in heredity. His numbers are small, but they show the characteristic increased vigor of  $F_1$  hybrids. The shorter average age of the lumped  $F_2$ 's indicates that there have segregated out in the  $F_2$  generation some short-lived flies. His data, however, do not give, or allow us to get, separate averages for the truncate  $F_2$ 's and the normal winged  $F_2$ 's.

His data are summarized in Table I.

In 1914 Baumberger (12) published a paper in which he gives data on the length of life of different orders of insects without food as affected by different constant temperatures, and by exposure to two different temperatures. Since the insects were caught in a net as imagoes the total

longevity is not known, so that the results have little significance from the standpoint of exact studies. The 359 insects had at 72° F. an average longevity of 4.8 days with a maximum of 15 days, at 62° F. an average of 6 days with a maximum of 23, and at 42° F. an average of 10.9 days with a maximum of 39. For the second part of the experiment 184 larvæ of the oak-tree moth were used. The results are too conflicting to allow one to draw any definite conclusions.

TABLE I

HYDE'S DATA ON INHERITANCE OF DURATION OF LIFE IN *DROSOPHILA*

Type of Flies		In-bred Wild	Truncate	F <sub>1</sub>	Truncate ♂ × Inbred ♀ F <sub>2</sub>	Reciprocal F <sub>2</sub>	Total
No. of Flies.		191	272	42	128	89	722
Mean duration of life in days.	♂ and ♀	37.4	21.4	47.0	29.5	29.3	.....
	♂	40.5	26.9	47.8	32.8	31.1	.....
	♀	34.5	18.5	46.4	25.9	27.3	.....

In 1915 appeared Lutz's (13) paper on natural selection in which he finds in each sex a slight negative correlation between the length of adult life and the duration of the embryonic periods. The distributions which he has for normal length of adult life with varying temperature give the 250 ♂s an average duration of life of 36.3 days, and the 263 ♀s an average of 28.9 days. He also gives distributions in hours of duration of life of flies which were given water but no food, and the correlations of duration of life of these starved flies with wing measurements.

During 1916 and 1917 Loeb and Northrop (14-16) published a series of papers on the effects of food and temperature on duration of life in *Drosophila*. The first preliminary paper in 1916 gives the duration of life of cultures of *Drosophila* in water and in cane sugar at temperatures from 28° to 9° C., showing a temperature coefficient for the duration of life of about the order of magnitude of that of chemical reactions, namely of about 2 for a dif-

ference of  $10^{\circ}$  C. The averages were much lower than those found by Hyde and Lutz because, of course, of the inadequate food. At  $19^{\circ}$  C. the culture in water had an average duration of life of 4.1 days and those in 1 per cent. cane sugar of 12.3 days. In 1917 the experiments were repeated, using sterile flies on 2 per cent. glucose agar which was found to be a more adequate food. Similar results were obtained, getting a similar coefficient for the duration of the larval and pupa stages, and finding that the ratios of the duration of the three different stages remained approximately constant for the different temperatures. The averages here of the life of the imago are more of the order of those found by previous workers, 228 flies at  $30^{\circ}$  lived an average of 13.6 days, 70 flies at  $25^{\circ}$ , 28.5, and 49 flies at  $20^{\circ}$ , 40.2. Later in 1917 they published another paper in which they give 92.4 days as the average duration of life of 143 flies at  $15^{\circ}$ , and 120.5 days of 105 flies at  $10^{\circ}$  C., together with the frequency distributions from which the averages were obtained. They also present results with different food mixtures, and for the two sexes separately, finding that isolated males live a little longer than isolated females, or than the males when mixed with females.

In another paper in the same issue Northrop (17) gives the results of some experiments undertaken to determine the effect on the duration of life of the imago of prolonging the life of the larva by inadequate feeding (omitting yeast for different lengths of time). In this way the embryonic periods were prolonged from 8 to 17 days, but the duration of life of the adult remained the same in every case, ranging between 10.5 and 11.9 days at  $27.5^{\circ}$  C., at which temperature the four experiments, involving 644 flies, were performed.

In a recent paper Arendsen Hein (18) gives a few observations on duration of life in the meal-worm *Tenebrio molitor*. Thirty-two male beetles lived an average of 60 days, with a range from 39 to 113, and 32 females averaged 111 days, with a range from 89 to 132 days.

## MATERIAL AND METHODS

The flies furnishing the data set forth in this paper belonged to five different basic laboratory stocks or strains of *Drosophila melanogaster*. Four of these stocks were obtained from Professor T. H. Morgan in December, 1919, and have been bred continuously in this laboratory since that time. The original individuals of the fifth stock were collected by one of us (R. P.) as wild flies at Eagle Point, Lake Memphremagog, Vermont, in the summer of 1920.

The stocks may be listed as follows:

1. *Old Falmouth*. Wild type fly, long bred in Morgan's laboratory. More inbred than 2.
2. *New Falmouth*. Wild type fly bred for about 6 months in Morgan's laboratory before we got our sample of it.
3. *Sepia*. A mutant stock carrying one third chromosome mutation, sepia eyes, in homozygous form. Other characters wild types. (Morgan.)
4. *Quintuple*. A synthetic stock, carrying five second chromosome mutations, each in homozygous form, as follows: Purple, arc, speck, vestigial, and black. Other characters wild type. (Morgan.)
5. *Eagle Point*. Wild type collected in summer of 1920, and since bred in this laboratory.

An account of the second chromosome mutations mentioned will be found in Bridges and Morgan (19) and Sturtevant (20). The discovery of the mutation sepia is noted by Muller (21).

The stocks are carried along in the laboratory in pure mass cultures in half-pint milk bottles. Those in an experiment on duration of life are tested relative to this character in one ounce shell vials.

The flies are all kept on a standard food mixture made up fresh each day, according to the following method:

For each 100 c.c. of water add 2 grams of agar-agar. Boil the agar and water until the agar is thoroughly dissolved. For each 100 c.c. of solution add 100 grams of ripe peeled mashed bananas. Boil five minutes. Pour into bottles which have been well heated in oven (or sterilized in autoclav). In the breeding bottles pour a layer  $\frac{3}{4}$  inch deep; in duration of life bottles a layer  $\frac{1}{2}$  inch deep. When

the food has partly cooled sprinkle on top of food the smallest possible amount of pulverized dry magic yeast (shaken from a can with one pin hole in cover). Put in breeding bottle a folded square of filter paper, and stopper with cotton batting.

The purpose of the filter paper is to furnish a dry place for the larvæ to crawl up and pupate on, and also to absorb some of the excess moisture which often forms on top of the food from the growing yeast. Filter paper has not been used in the small duration of life bottles, since no young are pupating there, and since it furnishes too many hiding places for the flies in the frequent transfers which have to be made in the duration of life tests. Excess of moisture on top of the food may become a source of error in duration of life experiments, because flies may drown in a small drop of water. Throughout our work we have been constantly on guard against this source of error and have tried a number of plans, with varying degrees of success to eliminate it entirely. Some of these experiments will be reported on in detail later on in this paper. In general it may be said here that this source of error from flies drowning need never be a significant one if due precautions are taken. We know that it has not been in our work.

Occasionally the yeast becomes too active at the edge of the food and causes the whole food mass to rise in the bottle. In an attempt to eliminate this accident yeast in dilute solutions was added to the boiled bananas and agar and was sprayed on top of the food. The results were not particularly favorable. The pulverized dry yeast added in the most minute quantity possible is the most satisfactory standard method yet found. We expect to continue attempting to get the food conditions more and more nearly ideal and identical in every experiment, but we feel reasonably certain that in all of the experiments we shall report, even including the very first in point of time, the precautions taken to standardize food and to guard against accidental death were sufficient to insure statistical accuracy in the results. Whatever environ-



mental differences in respect of food have existed in our experiments have been randomly distributed among the different groups in any given experiment. We have had very little trouble at any time with moulds in the cultures, the frequent transfers in the duration of life bottles in an experiment preventing them from getting any start.

The stock bottles holding reserve stocks of flies have been kept at the varying temperature of the room, but all experimental flies have been kept in electric incubators at 25° C., in which recording thermometers have been placed to insure that no fluctuations of temperature have occurred without our knowledge. All the experiments on duration of life and their results recorded in this paper have been carried through at the constant temperature of 25° C. We have settled on this as a normal for this particular element of the environmental complex.

During the first year of the experimental work no attempt was made to keep the different generations separate in the stock bottles, the process being merely to keep enough bottles (generally 4) of each stock to insure always having pupæ and newly emerging flies on hand for any matings and experiments to be started. Each week all the flies old and young together from the oldest bottle of each stock were transferred to a fresh bottle. In this way each bottle was kept 4 weeks and there were always on hand bottles with flies in all stages of development.

In January, 1921, it was decided that it would be desirable to keep the generations separate in the stock bottles. All stock bottles were emptied on January 11, and flies in the stock bottles on January 14 were arbitrarily called generation O. From that time on the procedure has been to empty out all the parent flies from each stock bottle 7 days after the bottle was started (when there are usually a large number of larvæ and some pupæ formed). The bottles are then left for 7 days longer, during which time enough flies emerge to start a fresh bottle for the next generation. Several bottles are kept of each stock, as

before, to insure always having on hand newly emerging flies with which to start experiments.

When any experiment is to be started flies are taken from the stock bottles and etherized within 4 hours of emerging (usually sooner), before the wings have unfolded, so that they are surely virgin. Matings are made up as desired, putting the mated flies in half-pint milk bottles in the incubator. The parents are taken from the mating bottles in 8 or 9 days (before any young begin to emerge), and removed to a second mating bottle if a larger sample of progeny is desired than can be obtained from one bottle. As the offspring begin emerging they are shaken out every morning from the mating bottle to a small shell vial. Thus all the flies in a small bottle are the same age, and are properly labelled with mating number and date of emergence. Then every morning all these small bottles are looked over and those with dead flies separated out. After all have been looked over, the live flies in the bottles which have dead ones are shaken across to fresh bottles, the dead flies taken out and sexed, and all the pertinent facts as to duration of life, etc., recorded on printed blanks, from which the records are later (when all the flies of an experiment have died off) coded, punched on Hollerith cards, and sorted and tabulated by Tabulating Machine Company electric sorting and tabulating machines. Flies from any small bottles which are not changed (because of dead flies) within five days of the last previous transfer are transferred on the fifth day to fresh food. The physical manipulation is too great with the numbers we desire to use to admit of changing all the bottles every day, which would be the ideal way to keep food conditions absolutely identical for all the flies. Changing every five days keeps them approximately so.

We desire to record our indebtedness to Mr. James Krucky, technical assistant in this work, for his painstaking care and fidelity to the highest ideals of exact experimental work.

In the work discussed in this paper no attempt has

been made to keep the flies in aseptic culture as had been done by Loeb and Northrop (*eve. cit.*) and other workers. Our choice in the matter has not been dictated by technical difficulties, which are not great, but has been deliberate. Aseptic life is by no means normal life for *Drosophila*. Normally it is as loaded with a bacterial flora as we are. It was felt that in the beginning it would be well to establish norms of duration of life for normal life conditions. Later we expect to make a special study of duration of life under aseptic conditions.

Duration of life in this work with *Drosophila* is always measured in days, and all of our records relate to duration of adult or imaginal life. No account is taken in any figures of the larval or pupal stages. The reason for this convention is first accuracy and second convenience. It is far more difficult to measure accurately either larval or pupal duration of life than it is imaginal. And from the point of view of these studies nothing significant in principle is lost by dropping these early stages, so far as we have been able to discover, either from the literature or experience with the flies.

#### MORTALITY CURVES

The most exact and comprehensive manner in which the facts about the duration of life in any organism can be presented is by means of life tables, of the type used for many years by actuaries in their work. The biologically essential features of a life table may be mentioned here briefly for the benefit of biologists not immediately familiar with the development of actuarial science. A complete life table includes, *inter alia*, the following items:

1. The number of individuals surviving up to each of the ages  $x_0$ ,  $x_1$ , etc., out of a given number (1,000 or 10,000 or whatever number one chooses) assumed to have started life together at exactly the same instant of time. These survival frequencies taken together constitute what is technically known as the  $l_x$  line of a life table.

2. The number of individuals dying within any short

interval of time, say between  $x$  and  $x + 1$ , or  $d_x = l_x - l_{x+1}$ . These frequencies of death taken together constitute the so-called  $d_x$  line of a life table.

3. The death rates at each time (or age)  $x$ ; *i.e.*, the ratio of the deaths between time  $x$  and  $x + 1$  to the survivors at the time  $x$ . These observations together constitute what is known as the  $q_x$  line of a life table  $q_x = (l_x - l_{x+1})/l_x$ .

4. The curtate expectation of life of individuals at a given age  $x$ . This is the mean or average after life time of all those individuals alive at age  $x$  neglecting fractions of the  $x$  interval. These observations together constitute the  $e_x$  line of a life table.

$$e_x = \frac{l_{x+1} + l_{x+2} + l_{x+3} + \text{etc.}}{l_x}$$

These simple definitions state with entirely sufficient accuracy for present purposes the significance of the constants which we shall present. Any one wishing to go more particularly into details of actuarial methods will find a useful elementary introduction in Henderson (22) or Dawson (23).

It is our purpose to present here life tables for four groups of flies, to serve, first, to show the general laws of mortality in *Drosophila* as compared with man, the only other organism for which we have extensive and exact life tables; and second, as a normal base for comparison in experimental work on *Drosophila* to be reported in subsequent papers.

The groups for which complete tables are presented are these:

1. *Long-winged males*. This table includes all our data up to June, 1921, on normal (*i.e.*, not experimentally modified) duration of life of male *Drosophila* individuals at 25° C. belonging to the following stocks (cf. p. 486 *supra*): Old Falmouth, New Falmouth, Sepia and Eagle Point. In these stocks all the individuals have wild type wings, hence the designation "long-winged."

2. *Long-winged females.* The corresponding table to 1, but for females.

3. *Short-winged males.* This table includes all our data up to June, 1921, on the normal duration of life at 25° C. of males belonging to the Quintuple stock. These flies carry the wing mutation vestigial; hence the designation "short-winged."

4. *Short-winged females.* The corresponding table to 3, but for females.

We have tried a number of different plans for the graduation of these tables, and wish to acknowledge gratefully the helpful suggestions of our colleague in the department, Dr. Lowell J. Reed, in connection with this phase of the work. It was first found that a rather satisfactory result could be obtained by fitting a logarithmic parabola of the type

$$y = a + bx + cx^2 + d \log x$$

to the  $q_x$  data. Working from this as a basis we finally decided that, as a practical matter, results on the whole most satisfactory could be got by the following type of graduation.

$$\log l_x = e a^x (a + bx + cx^2 + dx^3). \quad (i)$$

This amounts to asserting that the instantaneous death rate increases with age as a modified logarithmic function of  $x$ .

The actual equations for the four calculated  $l_x$  lines of Tables II to V inclusive, together with the absolute number of individuals on which the curves are based, are as follows:

*Long winged ♂s* (4,586 flies):

$$\log l_x = e^{.00838509x} (3.0041905 - .02937911x + .000140245x^2 - .0000015897x^3). \quad (ii)$$

*Long winged ♀s* (5,426 flies):

$$\log l_x = e^{.00181563x} (3.0042303 - .01869993x + .000059620x^2 - .0000020438x^3). \quad (iii)$$

*Short winged ♂s* (854 flies):

$$\log l_x = e^{.05718977x} (3.0085931 - .17931770x + .004010630x^2 - .0000332501x^3). \quad (iv)$$

*Short winged ♀s* (906 flies):

$$\log l_x = e^{.04604387x} (3.0116555 - .14948615x + .002851219x^2 - .0000210642x^3). \quad (v)$$

The plan of arrangement of Tables II to V is as follows: The first column gives the age of the flies in days, starting theoretically from the time of the emergence of the imago from the pupa as zero. Since the flies spend on the average a day in the breeding bottle before they are taken out into the small duration-of-life bottles, and the deaths are not observed for this interval, our distributions as recorded actually start with age 1 instead of age 0. The next two columns give the *observed* deaths and survivors on the basis of a thousand individuals at "birth" (here emergence as imago). The next three columns give the *calculated* (graduated) values deduced from equations (ii) to (v) above; first the  $l_x$  line, next the  $q_x$ , and finally the  $e_x$ , the latter values being of course in days. Owing to the fact that no premium rates are likely to be calculated from these life tables, we have not thought it necessary to keep but one place of decimals in the case of the  $q_x$  and  $e_x$  lines, and none whatever in the  $l_x$  line. Of course, in the computations more decimal places were kept, and these life tables may be regarded as accurate to a considerably higher degree than the figures as here published indicate. But, on the other hand, so far as we can see, the figures here tabled are sufficiently detailed for any use to which they are ever likely to be put.

The  $l_x$  lines of Tables II to V are shown graphically in Figs. 1 and 2. The diagrams are plotted to an arithlog grid, the scale of the abscissæ being divided arithmetically, and that of the ordinates logarithmically. Field (24) has shown the advantages of this method of plotting life table  $l_x$  lines. He says:

In the natural-scale diagram the descent of the curve expresses the number of deaths in a year among the survivors to a given age. This is not the usual way of stating death-rates; nor is it a convenient method, since the absolute number of deaths is a joint resultant of two factors which might better be considered separately—the probability of death at the specified age, and the number of persons at that age and subject to that hazard. We are ordinarily more concerned with the probability alone, or, which is much the same

TABLE II  
LIFE TABLE FOR DROSOPHILA—LONG-WINGED MALES

Age in Days	Observed		Calculated			Age in Days	Observed		Calculated		
	$d_x$	$l_x$	$l_x$	$q_x$	$e_x$		$d_x$	$l_x$	$l_x$	$q_x$	$e_x$
1.....	5	1,000	1,000	9.6	41.0	50.....	15	363	368	45.8	14.2
2.....	12	995	990	9.7	40.4	51.....	20	348	351	47.7	13.8
3.....	6	983	981	9.7	39.7	52.....	19	328	334	49.6	13.5
4.....	13	977	971	9.7	39.1	53.....	22	309	318	51.6	13.1
5.....	10	964	962	9.9	38.5	54.....	16	287	301	53.7	12.8
6.....	10	954	952	10.0	37.9	55.....	13	271	285	55.7	12.4
7.....	15	944	943	10.1	37.2	56.....	19	258	269	57.9	12.1
8.....	9	929	933	10.3	36.6	57.....	12	239	254	60.2	11.8
9.....	9	920	924	10.4	36.0	58.....	19	227	238	62.5	11.5
10.....	9	911	914	10.6	35.4	59.....	13	208	224	64.8	11.2
11.....	12	902	904	10.8	34.7	60.....	12	195	209	67.3	10.9
12.....	8	890	895	11.0	34.1	61.....	18	183	195	69.8	10.6
13.....	8	882	885	11.3	33.5	62.....	8	165	181	72.4	10.3
14.....	11	874	875	11.6	32.8	63.....	13	157	168	75.2	10.1
15.....	8	863	865	12.0	32.2	64.....	12	144	156	77.9	9.8
16.....	14	855	854	12.2	31.6	65.....	13	132	143	80.8	9.5
17.....	8	841	844	12.6	31.0	66.....	14	119	132	83.6	9.3
18.....	13	833	833	13.0	30.3	67.....	7	105	121	86.7	9.0
19.....	10	820	822	13.4	29.7	68.....	8	98	110	89.8	8.8
20.....	11	810	811	13.9	29.1	69.....	5	90	100	92.9	8.6
21.....	16	799	800	14.4	28.5	70.....	8	85	91	96.1	8.4
22.....	6	783	789	14.9	27.9	71.....	5	77	82	99.6	8.1
23.....	13	777	777	15.4	27.3	72.....	7	72	74	102.9	7.9
24.....	11	764	765	16.0	26.7	73.....	8	65	67	106.4	7.7
25.....	11	753	753	16.6	26.2	74.....	3	57	59	110.0	7.5
26.....	10	742	740	17.3	25.6	75.....	9	54	53	113.8	7.3
27.....	10	732	727	17.9	25.0	76.....	2	45	47	117.3	7.1
28.....	14	722	714	18.7	24.4	77.....	8	43	41	121.5	6.9
29.....	11	708	701	19.4	23.9	78.....	4	35	36	125.4	6.8
30.....	15	697	687	20.2	23.3	79.....	4	31	32	129.2	6.6
31.....	13	682	673	21.1	22.8	80.....	3	27	28	133.6	6.4
32.....	11	669	659	21.9	22.3	81.....	3	24	24	137.5	6.3
33.....	15	658	645	22.9	21.8	82.....	4	21	21	142.0	6.1
34.....	7	643	630	23.8	21.2	83.....	2	17	18	146.4	5.9
35.....	18	636	615	24.8	20.7	84.....	1	15	15	151.0	5.8
36.....	15	618	600	25.8	20.2	85.....	2	14	13	156.2	5.7
37.....	19	603	584	26.9	19.7	86.....	2	12	11	160.2	5.5
38.....	13	584	569	28.1	19.3	87.....	1	10	9	164.5	5.4
39.....	22	571	553	29.3	18.8	88.....	2	9	8	170.6	5.2
40.....	15	549	536	30.5	18.3	89.....	2	7	6	175.6	5.1
41.....	13	534	520	31.8	17.9	90.....	0	5	5	180.4	5.0
42.....	23	521	503	33.2	17.4	91.....	1	5	4	185.0	4.9
43.....	19	498	487	34.5	17.0	92.....	1	4	3	189.7	4.8
44.....	22	479	470	36.0	16.6	93.....	1	3	3	196.3	4.6
45.....	18	457	453	37.5	16.1	94.....	0	2	2	201.8	4.5
46.....	22	439	436	39.0	15.7	95.....	1	2	2	207.5	4.4
47.....	19	417	419	40.7	15.3	96.....	0	1	1	212.8	4.3
48.....	15	398	402	42.3	14.9	97.....	0	1	1	218.3	4.2
49.....	20	383	385	44.0	14.6						

TABLE III  
LIFE TABLE FOR DROSOPHILA—LONG-WINGED FEMALES

Age in Days	Observed		Calculated			Age in Days	Observed		Calculated		
	$d_x$	$l_x$	$l_x$	$q_x$	$e_x$		$d_x$	$l_x$	$l_x$	$q_x$	$e_x$
1.....	5	1,000	1,000	9.7	38.8	46.....	19	386	384	46.4	14.3
2.....	14	995	990	9.7	38.1	47.....	19	367	367	48.3	13.9
3.....	10	981	981	9.8	37.5	48.....	13	348	349	50.2	13.6
4.....	13	971	971	9.9	36.9	49.....	23	335	331	52.1	13.2
5.....	12	958	961	10.0	36.2	50.....	16	312	314	54.1	12.9
6.....	10	946	952	10.1	35.6	51.....	20	296	297	56.1	12.6
7.....	13	936	942	10.3	34.9	52.....	15	276	281	58.2	12.3
8.....	8	923	932	10.5	34.3	53.....	15	261	264	60.4	12.0
9.....	11	915	923	10.8	33.6	54.....	17	246	248	62.6	11.7
10.....	13	904	913	11.0	33.0	55.....	11	229	233	64.9	11.4
11.....	12	891	903	11.4	32.4	56.....	17	218	218	67.2	11.1
12.....	6	879	892	11.8	31.7	57.....	13	201	203	69.6	10.8
13.....	9	873	882	12.1	31.1	58.....	12	188	189	72.0	10.5
14.....	12	864	871	12.4	30.4	59.....	15	176	175	74.5	10.3
15.....	8	852	861	12.9	29.8	60.....	12	161	162	77.1	10.0
16.....	12	844	849	13.3	29.2	61.....	11	149	150	79.8	9.8
17.....	9	832	838	13.9	28.6	62.....	11	138	138	82.4	9.6
18.....	11	823	827	14.4	28.0	63.....	9	127	126	85.1	9.3
19.....	17	812	815	15.0	27.4	64.....	9	118	116	87.9	9.1
20.....	10	795	802	15.6	26.8	65.....	12	109	105	90.8	8.9
21.....	22	785	790	16.2	26.2	66.....	10	97	96	93.8	8.7
22.....	10	763	777	16.9	25.6	67.....	7	87	87	96.7	8.5
23.....	16	753	764	17.6	25.0	68.....	11	80	78	99.8	8.3
24.....	14	737	751	18.4	24.4	69.....	5	69	71	102.9	8.1
25.....	10	723	737	19.2	23.9	70.....	10	64	63	106.2	7.9
26.....	12	713	723	20.1	23.3	71.....	3	54	57	109.2	7.7
27.....	14	701	708	20.9	22.8	72.....	7	51	50	112.5	7.5
28.....	18	687	693	21.9	22.2	73.....	3	44	45	115.9	7.3
29.....	16	669	678	22.9	21.7	74.....	4	41	40	119.4	7.2
30.....	16	653	663	23.9	21.2	75.....	5	37	35	123.0	7.0
31.....	12	637	647	24.9	20.7	76.....	1	32	31	126.2	6.8
32.....	13	625	631	26.0	20.2	77.....	7	31	27	130.2	6.7
33.....	15	612	614	27.2	19.7	78.....	4	24	23	133.4	6.5
34.....	14	597	597	28.4	19.2	79.....	1	20	20	137.5	6.4
35.....	18	583	581	29.6	18.8	80.....	3	19	17	141.6	6.2
36.....	17	565	563	30.9	18.3	81.....	2	16	15	144.9	6.1
37.....	16	548	546	32.2	17.9	82.....	4	14	13	149.0	6.0
38.....	17	532	528	33.6	17.4	83.....	1	10	11	153.0	5.8
39.....	19	515	511	35.0	17.0	84.....	1	9	9	157.8	5.7
40.....	17	496	493	36.5	16.6	85.....	1	8	8	161.5	5.6
41.....	15	479	475	38.0	16.2	86.....	2	7	6	164.9	5.4
42.....	13	464	457	39.7	15.8	87.....	0	5	5	169.7	5.3
43.....	15	441	439	41.2	15.4	88.....	1	5	4	173.3	5.2
44.....	21	426	420	42.9	15.0	89.....	1	4	4	180.1	5.1
45.....	19	405	402	44.6	14.6	90.....	0	3	3	183.6	5.0
						91.....	1	3	2	188.7	4.9
						92.....	0	2	2	192.1	4.8
						93.....	1	2	2	195.1	4.7
						94.....	0	1	1	204.5	4.6
						95.....	0	0	1	209.5	4.5



TABLE IV  
LIFE TABLE FOR *DROSOPHILA*—SHORT-WINGED MALES

Age in Days	Observed		Calculated			Age in Days	Observed		Calculated		
	$d_x$	$l_x$	$l_x$	$q_x$	$e_x$		$d_x$	$l_x$	$l_x$	$q_x$	$e_x$
1.....	6	1,000	1,000	25.6	14.2	24.....	16	151	155	107.5	8.0
2.....	27	994	974	31.5	13.6	25.....	13	135	139	107.3	7.8
3.....	30	967	944	37.5	13.0	26.....	11	122	124	107.1	7.7
4.....	34	937	908	43.3	12.4	27.....	6	111	111	107.2	7.5
5.....	38	903	869	48.9	12.0	28.....	20	105	99	107.3	7.2
6.....	36	865	826	54.6	11.5	29.....	8	85	88	107.9	7.0
7.....	85	829	781	60.0	11.1	30.....	7	77	79	109.2	6.7
8.....	66	744	734	65.5	10.8	31.....	13	70	70	111.1	6.4
9.....	55	678	686	70.4	10.5	32.....	7	57	62	114.5	6.1
10.....	52	623	638	75.2	10.2	33.....	9	50	55	119.3	5.8
11.....	44	571	590	79.8	9.9	34.....	5	41	49	126.2	5.4
12.....	48	527	543	84.0	9.7	35.....	4	36	42	135.4	5.0
13.....	21	479	497	87.9	9.5	36.....	6	32	37	147.4	4.7
14.....	49	458	454	91.5	9.3	37.....	4	26	31	162.7	4.3
15.....	53	409	412	94.8	9.1	38.....	1	22	26	182.2	3.9
16.....	43	356	373	97.7	9.0	39.....	6	21	21	206.2	3.6
17.....	24	313	337	100.2	8.9	40.....	2	15	17	234.7	3.3
18.....	28	289	303	102.1	8.7	41.....	4	13	13	268.6	3.0
19.....	22	261	272	104.1	8.6	42.....	1	9	10	308.0	2.7
20.....	19	239	244	105.3	8.5	43.....	2	8	7	352.9	2.4
21.....	24	220	218	106.3	8.4	44.....	5	6	4	403.0	2.2
22.....	17	196	195	106.8	8.3	45.....	0	1	3	457.9	2.0
23.....	28	179	174	107.2	8.1	46.....	0	1	1	516.0	1.8

thing, with the proportion of those persons of given age who die in the course of a year. Precisely this relative mortality rate determines the slope of the curve in the logarithmic figure, for here, as always, a given distance on the logarithmic scale denotes a certain proportion of change. Hence the more steeply the logarithmic curve descends, the higher is the relative mortality which it indicates. Hence, too, it is possible to provide a key to the diagram in the form of standard sample slopes and corresponding numerical death-rates, which hold true for all parts of the curve.

From these tables and the diagrams, the following points are to be noted:

1. It is obvious that the laws of mortality are fundamentally similar in *Drosophila* to what they are in man, with the one striking and outstanding difference that since in the case of the *Drosophila* life tables we are deal-

TABLE V  
LIFE TABLE FOR *DROSOPHILA*—SHORT-WINGED FEMALES

Age in Days	Observed		Calculated			Age in Days	Observed		Calculated				
	$d_x$	$l_x$	$l_x$	$q_x$	$e_x$		$d_x$	$l_x$	$l_x$	$q_x$	$e_x$		
1.....	10	1,000	1,000	30.2	15.8	27.....	13	177	165	93.1	8.5		
2.....	26	990	970	33.9	15.2	28.....	18	164	149	94.6	8.3		
3.....	37	964	937	37.6	14.7	29.....	11	146	135	96.1	8.0		
4.....	31	927	902	41.2	14.3	30.....	20	135	122	98.1	7.8		
5.....	47	896	865	44.7	13.9	31.....	15	115	110	100.2	7.5		
6.....	27	849	826	48.1	13.5	32.....	15	100	99	102.8	7.2		
7.....	50	822	786	51.5	13.1	33.....	8	85	89	106.3	6.9		
8.....	78	772	746	54.7	12.7	34.....	5	77	80	110.0	6.6		
9.....	45	694	705	57.9	12.4	35.....	7	72	71	114.5	6.3		
10.....	63	649	664	60.9	12.1	36.....	10	65	63	120.2	6.0		
11.....	34	586	624	63.8	11.8	37.....	6	55	55	127.1	5.7		
12.....	35	552	584	66.6	11.6	38.....	7	49	48	134.8	5.4		
13.....	25	517	545	69.2	11.3	39.....	8	42	42	144.4	5.1		
14.....	39	492	507	71.7	11.1	40.....	8	34	36	155.8	4.8		
15.....	31	443	471	74.1	10.9	41.....	8	26	30	168.4	4.5		
16.....	30	412	436	76.2	10.7	42.....	3	18	25	183.8	4.2		
17.....	28	382	403	78.3	10.5	43.....	1	15	20	201.3	3.9		
18.....	28	354	371	80.2	10.3	44.....	3	14	16	221.2	3.6		
19.....	25	326	341	82.0	10.1	45.....	1	11	13	243.8	3.3		
20.....	14	301	313	83.6	9.9	46.....	0	10	10	269.9	3.1		
21.....	20	287	287	85.1	9.7	47.....	2	10	7	297.0	2.8		
22.....	14	267	263	86.6	9.5	48.....	0	8	5	328.9	2.6		
23.....	21	253	240	87.9	9.3	49.....	2	8	3	363.3	2.4		
24.....	21	232	219	89.2	9.1	50.....	3	6	2	401.0	2.2		
25.....	16	211	199	90.4	8.9	51.....	1	3	1	457.2	2.0		
26.....	18	195	181	91.7	8.7								

ing only with the duration of imaginal life, the important infant and early childhood mortality component of the human  $d_x$  line is entirely omitted. With this difference in mind, it is apparent that the remainder of the  $l_x$  curve for the flies is essentially similar to any human  $l_x$  curve. Further on, we shall make a more detailed comparison between *Drosophila* and human curves.

2. There is evidently a fundamental and marked difference between the long-winged and short-winged groups in respect of the duration of life. This difference is somewhat more marked in the case of the males (Fig. 1) than in the females, but it is sufficiently definite and clear-cut

FIG. 1. Diagram showing the observed and graduated  $l_x$  points for long-winged and short-winged males, respectively. The small circles are the observations and the smooth lines the fitted curves from equations (ii) and (iv). In order not to overcrowd the diagram, only every second observation is shown.

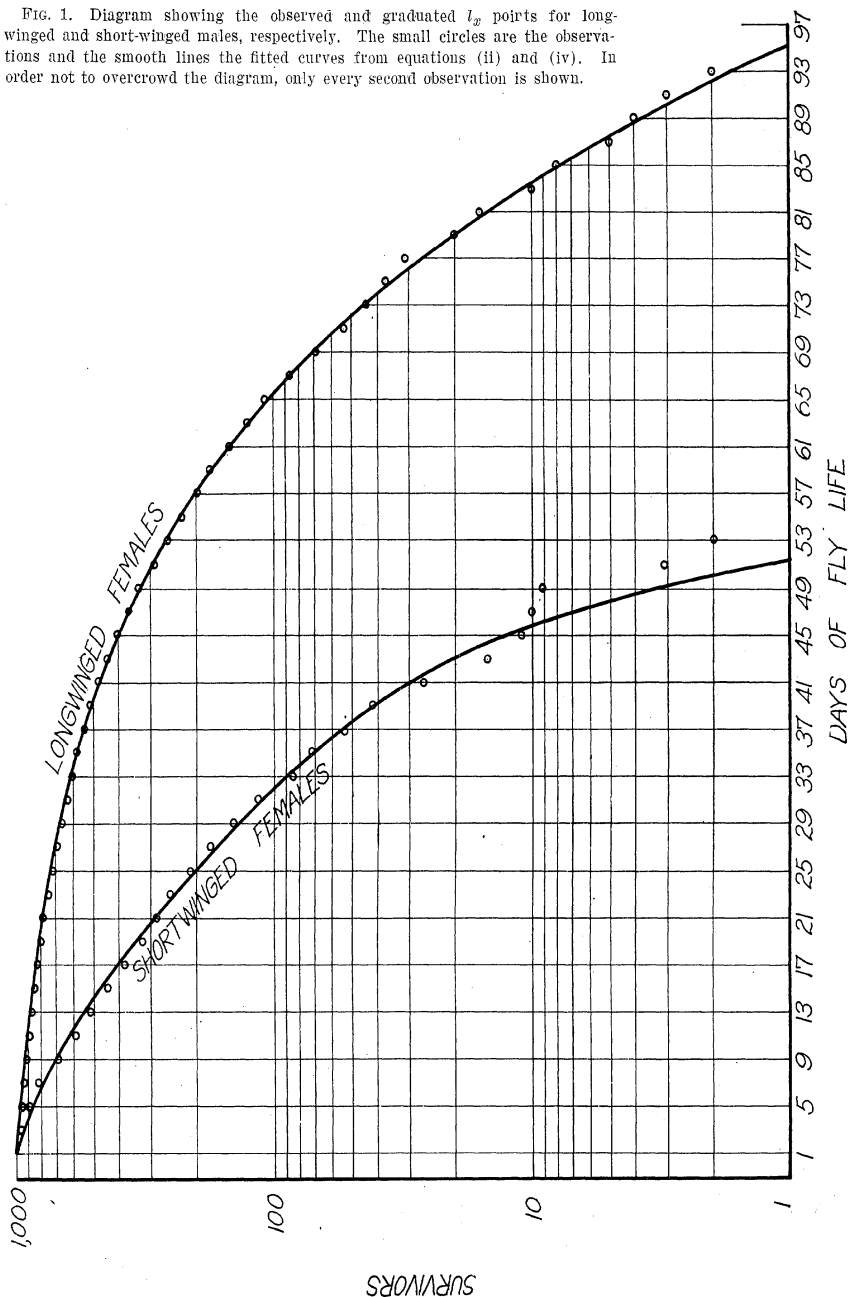
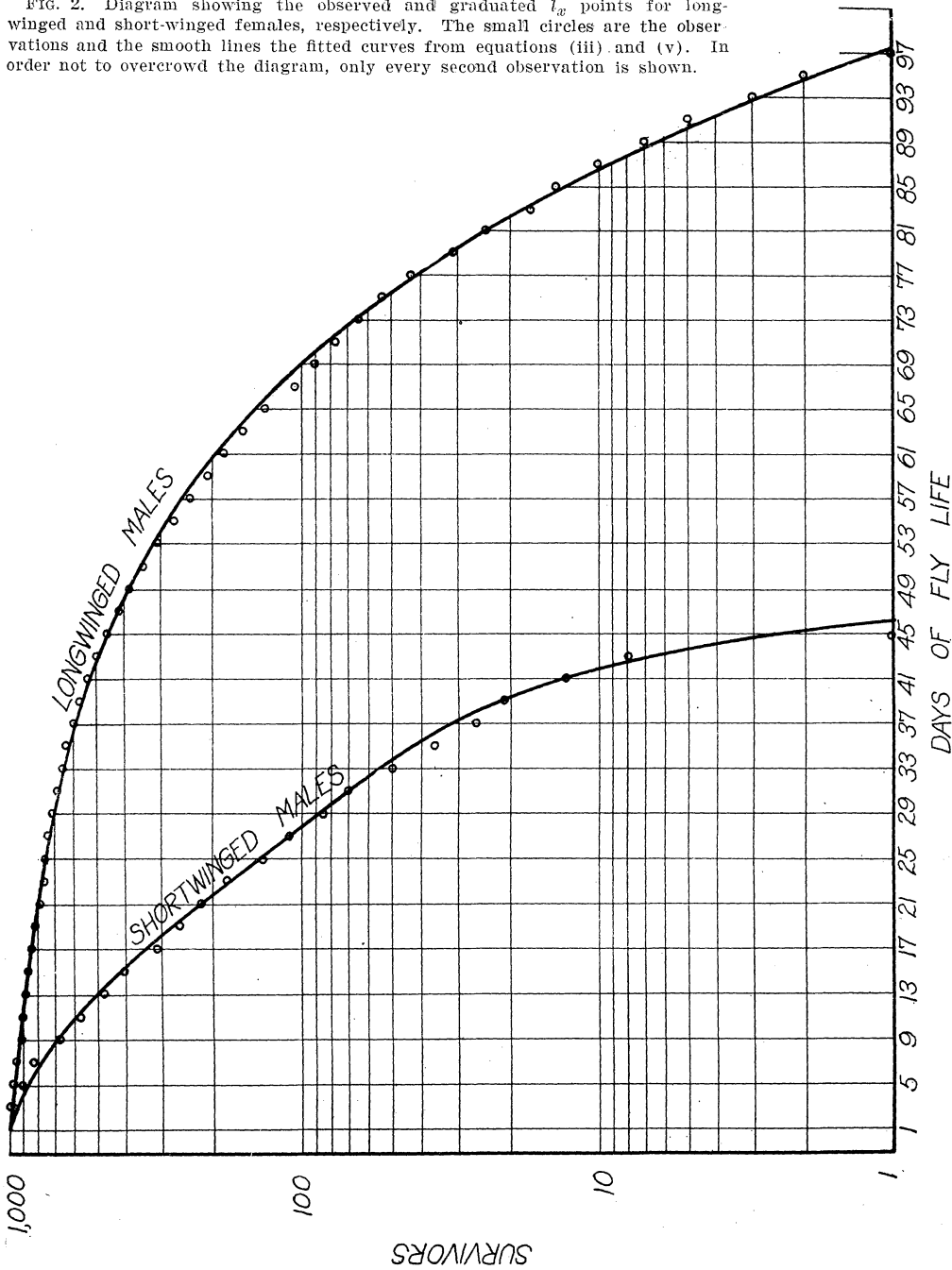


FIG. 2. Diagram showing the observed and graduated  $l_x$  points for long-winged and short-winged females, respectively. The small circles are the observations and the smooth lines the fitted curves from equations (iii) and (v). In order not to overcrowd the diagram, only every second observation is shown.



in both cases. Broadly speaking, the wild type long-winged flies have from two to three times as great an expectation of life at any age as do the flies of the Quintuple stock. Since all of these flies lived under substantially identical environmental conditions, as has been set forth earlier, it follows that the basis of the great difference in expectation of life between these two groups, as exemplified in Figs. 1 and 2, is *hereditary and not environmental*.

3. It is apparent that on the whole the graduations given by equations of the type of (i) are very satisfactory, and as good as could reasonably be expected on experience bases of the magnitude of those here dealt with. Undoubtedly the curves would be slightly more smooth if we had larger experience, especially in Tables IV and V, where we are dealing with less than a thousand flies in each case, but in the main the curves fit the observations very well.

4. The death rates ( $q_x$ ) generally increase steadily with advancing age. An exception to this rule is the slight dip between ages 25–28 in the short-winged ♂ table.

In Figs. 3 and 4 the *Drosophila l<sub>x</sub>* lines are compared with the human  $l_x$  line taken from Glover's (25) 1910 U. S. Life Tables. In order to make a just comparison, the human  $l_x$  line is displaced to the left in the diagrams until age fifteen of human life coincides with age one of the fly curve. This drops out the infant and childhood mortality component of the human curve. It will be understood that in the present instance, this is a somewhat arbitrary and purely graphic procedure. Whether the point which *exactly* corresponds on the human curve to the beginning of the *Drosophila* imago curve is exactly 15 years or 13 or 14, or some other near-by value, is a matter for further research. In a broad way, however, it is clear that the two lines must be taken to correspond at something like this point in the human curve.

From these diagrams, it is apparent that, after leaving out the infant mortality component of the human curve,

the essential difference between the human and *Drosophila*  $l_x$  curves is that, up to what may be designated as the end of the middle life portion (and even into the early part of the old age portion), human beings have a *relatively* better expectation of life than does *Drosophila*. On the other hand, in the extreme old age portion of the curve, the *Drosophila* expectation of life is relatively

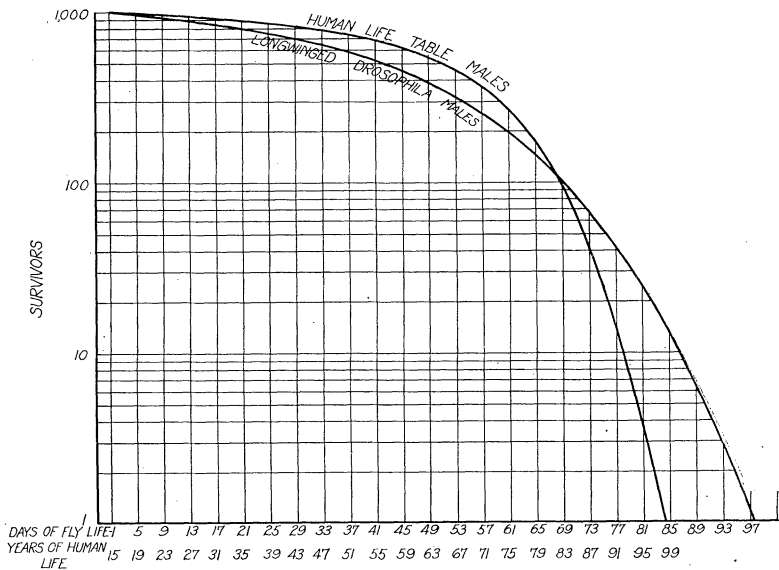


FIG. 3. A comparison of human  $l_x$  and *Drosophila*  $l_x$  lines for males.

better than the human. The result then is as though some external power had seized the *Drosophila*  $l_x$  line at about the middle of its course and bent it to a sharper angle in that region, stretching it at that point upward and to the right and by this process converted it into the human curve. Suppose one of the *Drosophila*  $l_x$  lines, as shown in Fig 3, to be a thin, flexible whalebone rod, possessing mass. Then move a point on that rod standing say just above the final *A* in "*Drosophila*" in Fig. 3, up to a point where it exactly coincides with the human life table curve. Then the whole of the rest of the *Drosophila* curve would fall into about the same posi-

tion as is occupied now by the human life table curve. Put in another way, what appears to have happened is that, as compared with *Drosophila*, more human beings are able to live through middle life, but at the expense of those who, if the mortality law was the same as in *Drosophila*, would live to extremely advanced old ages. As a matter purely of speculation in the present stage of our knowledge, it may be suggested that the *Drosophila*

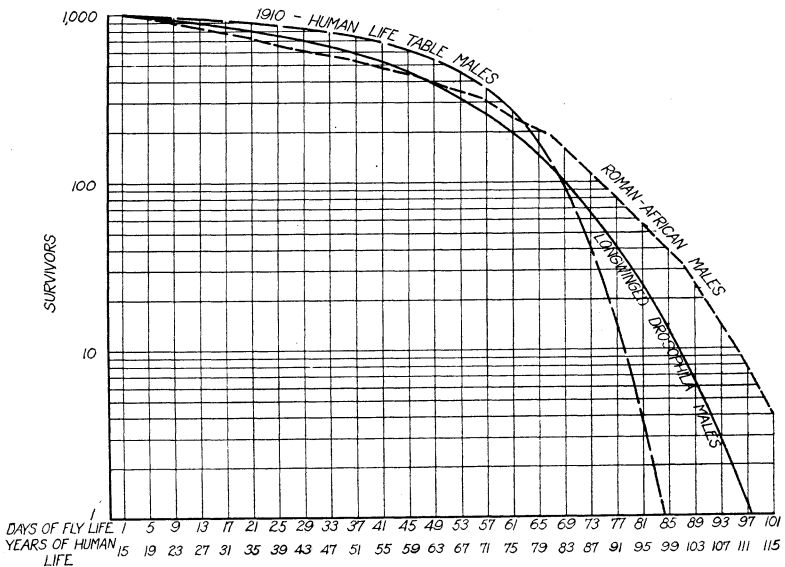


FIG. 4. A comparison of human  $l_x$  and *Drosophila*  $l_x$  lines for females.

$l_x$  curves represent more nearly the normal, fundamental, biological law of mortality, and that the human curve has been warped from this form as a result of those activities which may be comprised under the terms public health and sanitation. It is to be understood that at present we offer this merely as a suggestion and in no way as a settled conclusion. It is, however, clear that the effect which we should expect these activities to have upon the form of the  $l_x$  line is exactly of the sort which makes the human curve different from the *Drosophila* in fact.

In this connection Fig. 5 is of interest and significance.

It compares, for males, two human  $l_x$  lines nearly 2,000 years apart in point of time, with the long-winged *Drosophila*  $l_x$  line of Table II. The two human lines are (a) Glover's, 1910 U. S. table (as in Fig. 3), and (b) Macdonell's (26) observed  $l_x$  line from the population of Roman provinces in Africa at about the beginning of the Christian era, his data having been taken from grave-stone inscriptions. We calculated the  $l_x$  line here plotted from Macdonell's tabled  $d_x$  data, determining an  $l_x$  point at each quinquennium. This smooths the Roman-African figures somewhat, and makes the  $l_x$  line so determined lie very slightly higher all along its course than would be the case if we used a more elaborate and exact mathematical procedure. The error, however, is so small that it would scarcely be discernible in the scale at which Fig. 5 is reproduced.

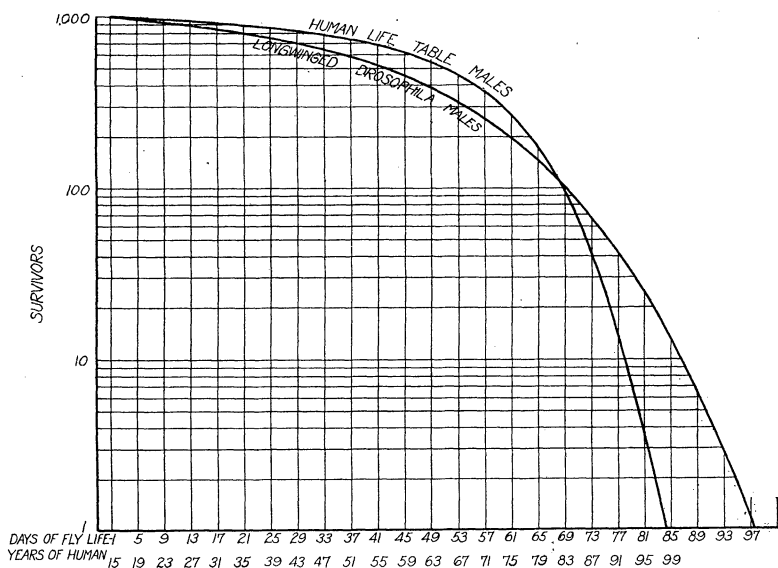


FIG. 5. A comparison of *Drosophila* mortality with human mortality at two periods (a) early in the Christian era, and (b) in 1910.

It is at once apparent from Fig. 5 that the *Drosophila* survival curve runs, in general throughout its course, *between* the curve for human beings 18 or 19 centuries



ago and that for the present time. As compared with Glover's 1910 U. S. tables, the Roman population of Africa at the dawn of our era was, in respect of the course of its mortality, even more *Drosophila*-like than *Drosophila* itself! Now in Roman Africa there was relatively little of what we now understand as sanitation, hygiene, and preventive medicine. Men lived to old age, if they did, by virtue mainly of the strength of their innate constitutions, and their good luck in avoiding fatal accidents. At the present time hospitalization, the science and art of medicine and public health, and general sanitation keep many persons alive well into middle age who would in those days have died much earlier because of a lack of constitutional ruggedness. Altogether the data of Fig. 5 seem highly significant in relation to the hypothesis suggested above as to the reason for the difference between *Drosophila* and man in respect of mortality curves.

#### ACCIDENTAL DEATHS

The tacit assumption in all the foregoing is that each of the 11,772 flies comprised in the four life tables died a natural death, and that the time of death (or duration of life) was in each case determined fundamentally by internal factors, since the environment was substantially a constant for all.

For certainly more than 98 per cent. of the flies this assumption is unquestionably true. But in view of the possibility that some few of the flies might be dying accidental deaths by drowning in the moisture, which sometimes collects on the surface of the food, it was thought worth while to attempt to prevent the collection of moisture in some of the bottles and compare the duration of life of flies kept in such bottles with that of flies kept under the ordinary conditions. Accordingly, bottles of food were prepared by putting discs of several layers of a very absorbent paper, Zorbik, in the bottom of the bottle and then pouring in the food and letting it solidify

on as steep a slant as possible, so that any moisture formed would drain down and be absorbed by the paper in the bottom of the bottle. Flies of generation 5 from four different lines were used in the experiment, two normal wild type lines, one of Old Falmouth stock and one of New Falmouth stock, and two lines of Quintuple stock. Flies were taken out from stock bottles of these lines as they emerged every day, beginning March 18, 1921, and continuing through April 4, putting hatches of alternate days in the specially prepared bottles and the other hatches in ordinary bottles. The flies put into the specially prepared bottles were of course kept throughout their lives in such bottles, and the controls in ordinary bottles. Table VI shows the  $l_x$  lines of the four groups of flies—long-winged with paper and slant food, long-winged without paper and food surface horizontal, short-winged with paper and slant food, short-winged without paper and food surface horizontal. Distributions have been made for the four lines separately, and for the sexes separately, but since they all show the same results the separate distributions are not given.

The data of Table VI are shown graphically in Fig. 6.

It is evident that there is no definite or marked difference between the slant food group and the other. Such differences as do appear between the  $l_x$  lines in the two cases are only of the order of magnitude which might readily appear in random sampling. This is indicated in another way by the data of Table VII.

In the case of the short-winged flies the difference in the mean is plainly not significant. In the case of the long-winged flies the difference is 2.96 times its probable error. One would expect a difference as great as this or greater to occur from chance alone only 4 to 5 times in every 100 trials, so that the difference is here getting on towards the magnitude where it must be regarded as certainly significant on purely statistical grounds. But the difference is in favor of the horizontal food without drainage, and *against* the food with drainage.

TABLE VI

SURVIVAL DISTRIBUTION OF FLIES UNDER DIFFERENT CONDITIONS AS TO  
SURFACE MOISTURE ON FOOD

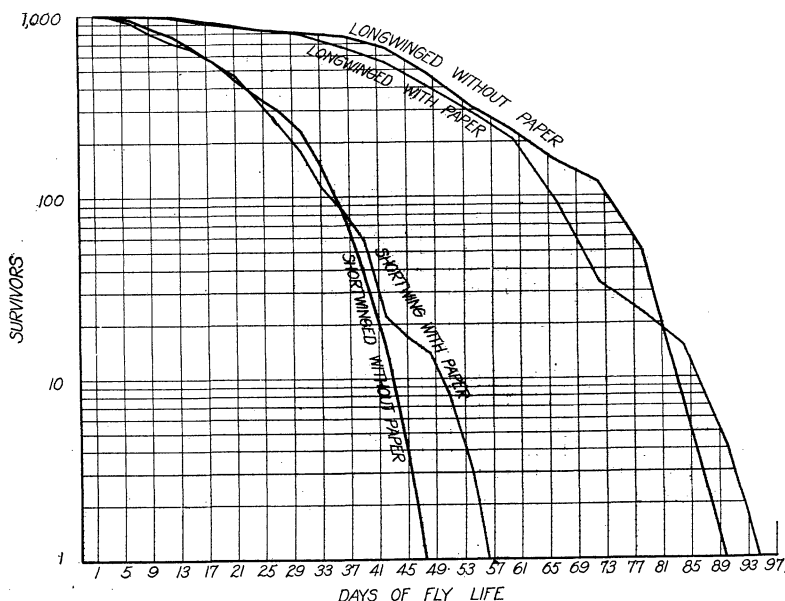
Age	Short-winged Flies		Long-winged Flies	
	With Paper and Slant Food	Without Paper. Food Surface Horizontal	With Paper and Slant Food	Without Paper. Food Surface Horizontal
1.....	1,000	1,000	1,000	1,000
3.....	983	1,000	—	—
6.....	913	951	996	1,000
9.....	804	857	—	—
12.....	712	774	974	982
15.....	651	660	—	—
18.....	556	498	898	912
21.....	469	442	—	—
24.....	346	355	834	832
27.....	257	302	—	—
30.....	182	234	796	799
33.....	115	147	—	—
36.....	84	83	675	770
39.....	59	38	—	—
42.....	22	15	547	661
45.....	17	4	—	—
48.....	14	0	408	482
51.....	8	—	—	—
54.....	3	—	294	314
57.....	0	—	—	—
60.....	—	—	204	230
63.....	—	—	—	—
66.....	—	—	94	157
69.....	—	—	—	—
72.....	—	—	34	120
75.....	—	—	—	—
78.....	—	—	23	51
81.....	—	—	—	—
84.....	—	—	15	7
87.....	—	—	—	—
90.....	—	—	4	0
Absolute number of flies.	(265)	(274)	(358)	(265)

On the whole it seems perfectly clear that these experiments give no justification for going to the considerably greater trouble of preparing this food so that there is drainage from its surface. As a matter of fact the drainage of moisture is never entirely complete even with

TABLE VII

MEAN DURATIONS OF LIFE CALCULATED FROM THE DATA OF TABLE VI

	Mean Duration of Life		Difference of Means	Diff. P.E. Diff.
	With Paper and Slant Food	Without Paper and Slant Food		
Long-winged . . . . .	43.80 $\pm$ .73	46.91 $\pm$ .75	3.10 $\pm$ 1.05	2.96
Short-winged . . . . .	20.10 $\pm$ .40	20.58 $\pm$ .42	.48 $\pm$ .58	.83

FIG. 6. Comparing survival ( $l_x$ ) lines under different food conditions explained in text.

the slant food and absorbing paper. Small drops still cling in some cases to the agar, and a fly might drown in such a drop just as well as in a similar drop on a horizontal surface. The important point is that this experiment confirms our general experience in this work, namely, that accidental deaths occur so extremely rarely under our conditions that they do not appreciably affect the results.

## SUMMARY

This paper is the first in a series of experimental studies on the factors influencing the duration of life in *Drosophila melanogaster*. An account of the experimental technique used in these duration of life studies is presented. Four complete life tables for *Drosophila* are given, and it is shown that this organism follows quantitatively the same general law in respect of the distribution of its mortality as does man. As this work deals only with the duration of imaginal life in *Drosophila* there is no component in the life tables corresponding to the mortality of infancy and childhood in man. It is shown that there are wide differences in duration of life in different stocks of *Drosophila*, and that the basis of these differences is hereditary and not environmental. The *Drosophila* survival line of the life table ( $l_x$ ) runs in general throughout its course between human survival lines of (a) the present time, and (b) about the beginning of the Christian era (Macdonell's data from Roman Africa), the curves being superposed on the basis of the omission of the human mortality of infancy and childhood.

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